RHODORA, Vol. 91, No. 868, pp. 296–314, 1989

CHROMOSOME NUMBER DETERMINATIONS IN FAM. COMPOSITAE, TRIBE ASTEREAE. III. ADDITIONAL COUNTS AND COMMENTS ON GENERIC LIMITS AND ANCESTRAL BASE NUMBERS

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ABSTRACT

Chromosome numbers of 261 individuals representing 121 taxa and 4 interspecific hybrids from 25 genera are reported. The majority of the counts are for *Aster, Gutierrezia* and *Solidago.* Nearly all counts confirm previous reports for the taxa; some reports are first counts for a state or province. Over 100 counts are from populations in California. Included are first reports for the following taxa: *Aster laevis* var. *guadalupensis,* $2n = 48$; *Aster priceae,* $2n = 64$; *Aster reticulatus,* $2n = 9_{II}$; *Aster wasatchensis,* $2n = 18$; *Gutierrezia solbrigii,* $2n = 20_{II}$; *Heterotheca jonesii,* $2n = 9_{II}$; *Heterotheca rutteri,* $2n = 18$; and *Stephanodoria tomentella,* $2n = 6_{II}$.

Key Words: Compositae, Astereae, chromosome numbers, *Aster, Gutierrezia, Haplopappus, Heterotheca, Solidago, Stephanodoria*

INTRODUCTION

Biosystematic studies are enhanced by knowledge of variation in chromosome number within and between taxa (Strother, 1972). Determining the distribution patterns of cytotypes requires numerous counts from the range of a taxon. Ideally, when a large number of counts from the entire range of a single species, or species complex, can be accumulated, a paper limited to that taxon is published (e.g., Semple and Chmielewski, 1985; Chmielewski and Semple, 1985). However, for most taxa a career is required to build such a data base, and therefore only a few counts for most taxa are reported at a time in order to make the information generally available. This is the third in a continuing series of miscellaneous chromosome number reports on Astereae by the first author's laboratory (Semple, 1985; Semple and Chmielewski, 1987).

MATERIALS AND METHODS

Meiotic counts were made from pollen mother cells dissected from buds fixed in the field in 3:1 EtOH : acetic acid, and subsequently stored under refrigeration in 70% EtOH. Mitotic counts were made from root tip cells taken from transplanted rootstocks or seedlings. Root tips were pretreated in 0.01% colchicine for 2–3 hr., fixed in Modified Carnoy's Fixative (4:3:1 chloroform : EtOH : acetic acid), and hydrolyzed in 1 N HCl for 30 min. at 60°C before squashing. Both meristematic root tips and anther sacs containing microsporocytes were squashed in 1% acetic orcein and chromosome counts were made from freshly prepared material. Permanent slides were made in most cases and remain in the possession of J.C.S. (following Semple et al., 1981) or M.A.L. (following Jackson, 1973).

Voucher specimens for all counts are deposited in WAT, TEX or COLO unless otherwise indicated in Table 1.

RESULTS AND DISCUSSION

The chromosome numbers of 261 individuals representing 121 taxa and 4 interspecific hybrids from 25 genera are reported for the first time (Table 1). The majority of the reports are for three genera: *Aster* (88 counts, not including *Virgulaster* and *Virgulus*), *Gutierrezia* (41 counts), and *Solidago* (73 counts). Populations were sampled in five provinces and territories in Canada, 29 states in the United States, five states in Mexico, and one province in Argentina. More than 100 of the collections were from California. All but a few counts are consistent with previous reports for the taxa and therefore are presented without comment. For most taxa too few counts have been reported to justify discussion of cytotype distribution patterns. Some counts are first reports for the taxon from a particular state; e.g., *Aster pilosus* var. *pringlei* ($2n = 48$) and *Solidago flexicaulis* ($2n = 36$) from Wisconsin, and *Virgulus pratensis* ($2n = 10$) from Florida.

The following are first reports for the taxon: *Aster laevis* L. var. *guadalupensis* A. G. Jones, $2n = 48$ (two populations); *Aster priceae* Britt., $2n = 64$ (five populations); *Aster reticulatus* Pursh, $2n = 9_{II}$ (three populations); *Aster wasatchensis* (M. E. Jones) Blake, $2n = 18$ (one population); *Gutierrezia solbrigii* Cabrera, $2n = 20_{II}$ (one population); *Heterotheca jonesii* (Blake) Welsh & Atwood, $2n = 9_{II}$ (one population); *Heterotheca rutteri* (Rothr. in Gray) Shinners, $2n = 18$ (one population); and *Stephanodoria tomentella* (Robinson) Greene, $2n = 6_{II}$ (four populations).

Table 1. Chromosome number determinations of Astereae from Canada and the United States (unless otherwise indicated from Mexico or Argentina), arranged alphabetically. Vouchers were collected by Semple & Heard unless otherwise indicated: *Bt* = L. Brouillet; *CC#* = C. C. Chinnappa et al. collection numbers; *Ch* = J. Chmielewski; *L* = M. A. Lane; *R* = G. Ringuis; *S* = J. Semple.

Acamptopappus shockleyi Gray. $2n = 9_{II}$. **Nevada.** Clark Co.: S of NV-157 on dirt rd. into Kyle Canyon, *L 3063.*

Aphanostephus skirrhobasis (DC.) Trel. var. *skirrhobasis.* $2n = 3_{II}$. **Texas.** San Patricio Co.: TX-361 0.5 mi W of Ingleside, *S 596* (MO).

Aster subg. *Aster* ($x = 9$ sections and subsections)

A. divaricatus L. $2n = 18$. **New York.** Cattaraugus Co.: US-219 7.6 km N of Ellicottville, *S & R 7569.*

A. integrifolius Nutt. $2n = 18$. **California.** Mono Co.: CA-108 6.2 km W of Leavitt Meadow Campground, *8728-2.*

A. macrophyllus L. $2n = 72$. **Pennsylvania.** Clearfield Co.: US-219 ca. 5 mi. S of Burnside, *S & R 7673.* Elko Co.: US-219 S of Wilcox, *S & R 7586, S & R 7587.*

A. oregonensis (Nutt.) Cronquist. $2n = 9_{II}$. **California.** Del Norte Co.: US-199 W of Gasquet, *8519.* Siskiyou Co.: For. Serv. Hwy 93 NW of Salmon Forks, *8479.* Sierra Co.: CA-94 9.1 km E of Downieville P.O., *8411.* Yuba Co.: ca. 9000 La Porte Rd. (Co.Rd-E21) near Brownsville, *8413.* $2n = 18$. **California.** Calaveras Co.: CA-4 8.3 km W of Bear Valley Rd., *8781.* Eldorado Co.: S of Fallen Leaf Lake, Camp Richardson, *S & Ch 8911.*

A. radulina Gray. $2n = 27 = 3x$. **California.** San Mateo Co.: CA-35 27.4 km S of CA-92, *S & Ch 8914.*

Aster subg. *Aster* sect. *Dumosi* ($x = 8$)

A. anomalus Engelmann. $2n = 16$. **Oklahoma.** Leflore Co.: OK-1 E of Talimena, *8270.*

A. borealis (Torr. & Gray) Prov. $2n = 16$. **Saskatchewan.** 2.5 mi. W of Carragana, *Hooper & Baker 83073122.* $2n = 32$. **Minnesota.** Aitkin Co.: MN-18 SW of McGrath, 4.0 km E of MN-65, *S 9068.*

A. bracteolatus Nutt. $2n = 16$. **California.** Siskiyou Co.: Mt. Shasta City, *8459.*

A. ciliolatus × *A. lanceolatus.* $2n = 48$. **Saskatchewan.** NE of Somme, *Hooper & Baker 84082601.*

A. cordifolius L. $2n = 16$. **Delaware.** New Castle Co.: DEL-82 S of Yorklin, *S & R 7623.* $2n = 32$. **Maine.** Washington Co.: ME-9 SW of Calais, *S & Keir 4904.* **Pennsylvania.** Bedford Co.: PA-26 N of Tatesville, *S & R 7672.* Mckeene Co.: Custer City, *S & R 7580.*

A. dumosus L. $2n = 16$. **Kentucky.** Allen Co.: US-231, 11.5 km W of US-31, *S & Ch 9108.* **South Carolina.** Chesterfield Co.: SC-109 5.9 mi. N of SC-145 N of Mckennon, *S & Ch 6078.* $2n = 32$. **Florida.** Okeechobee Co.: Fl-70 2 mi. E of Okeechobee, *S et al. 7511.*

A. laevis L. var. *guadalupensis* A. G. Jones. $2n = 24_{II}$. **Texas.** Culberson Co.: Guadalupe Mountain National Park, Bowl Trail, *8179.* $2n = 48$. **Texas.** Culberson Co.: Guadalupe Mountain National Park, *8183.*

A. laevis L. var. *laevis.* $2n = 48$. **Michigan.** Crawford Co.: US-27 2 mi. S of Otsego Co., *S & Ch 4978.* Delta Co.: US-421 4.7 km E of Bank R., *S & Ch 5022.*

Table 1. Continued.

Mackinac Co.: Pt. aux Chenes, *S & Ch 5001.* Roscommon Co.: US-27 5 mi. S of Crawford Co., *S & Ch 4977.* **Minnesota.** Lincoln Co.: US-75 S of Lake Benton, *S & Ch 5132.* **Missouri.** Harrison Co.: US-136 W of Bethany, *S & Ch 5233.* **Pennsylvania.** Centre Co.: PA-144 W of Pleasant Gap, Nittany Mts., *S & R 7600.* **Wisconsin.** Douglas Co.: WI-27 2.1 km N of Co.Rd-2A, WNW of Barnes, *S 9081.*

A. lanceolatus Willd. ssp. *hesperius* (Gray) Semple & Chmielewski. $2n = 64$. **North Dakota.** Barnes Co.: Valley City, *S & Bt 6956.*

A. lanceolatus ssp. *lanceolatus.* $2n = 64$. **New York.** Cortland Co.: NY-281 2 mi. NE of Preble, *S 6799.* Onondago Co.: junction of US-20 and I-81, *S 6798.*

A. lanceolatus spp. *lancelatus* × *A. pilosus.* $2n = 48$. **Ontario.** Bruce Co.: 18.2 km S of Gilles Hill, *Ch 2028.*

A. lateriflorus L. var. *lateriflorus.* $2n = 16$. **Minnesota.** Mille Lacs Co.: US-169 between Rum River Rest Area and road to Onamia, *S 9065.*

A. lateriflorus L. var. *tenuipes* Wieg. $2n = 16$. **Ontario.** Renfrew Co.: NW of Deep River, along Ottawa R. 300 m NW of Mcfarlanes Point, *Brunton & McIntosh 7536.*

A. lentus Greene. $2n = 32_{II}$. **California.** Napa Co. Napa City, corner of Big Ranch Rd. and Trancas St., *8579.*

A. lowrieanus Porter. $2n = 16$. **Tennessee.** Cocke Co.: Co.Rd NW of Hartford, *S, Brammall & Hart 3015.*

A. occidentalis Nutt. $2n = 16$. **California.** Mono Co.: E of Tioga Pass, Aspen Grove Campground, *8715*; CA-108 W of West Walker R., *8721.* Plumas Co.: SW of Crescent Mills, *S et al. 5717a.* $2n = 32$. **California.** Mono Co.: Tioga Pass 0.25 mi. E of Yosemite National Park, *8690.* Siskiyou Co.: SE of Etna, CA-3 at rd. to Gazelle, *8499.* **Idaho.** Custer Co.: W of Sunbeam, *S & Bt 7051.* **Oregon.** Lane Co.: Willamette N.F., OR-242, 11.9 mi. E of OR-126, *S & Bt 7166.* $2n = 40$. **California.** Plumas Co.: SW of Crescent Mills, *S et al. 5717b.*

A. ontarionis Wiegand. $2n = 32$. **Ontario.** Brant Co.: Paris, *Ch 1431.* **Kentucky.** Warren Co.: US-213 10.9 mi. SE of I-65 (Bowling Green), *S & Ch 9104.*

A. pilosus Willd. var. *pilosus.* $2n = 32$. **Ontario.** Lambton Co.: Bosanquet Twp, Ipperwash Rd., *Ch 2239*; entrance to Ipperwash Provincial Park, *Ch 2240.* **Tennessee.** Rutherford Co.: E of Silver Hill on Al Sup Mill Rd., *S & Ch 9113.*

A. pilosus Willd. var. *pringlei* (Gray) Blake. $2n = 48$. **Ontario.** Halton Co.: S of Moffatt, *Ch 2374.* Niagara Reg. Mun.: N of Snyder, junction of Sommerville Rd. and Sodom Rd., *Ch 1754, 1755.* Manitoulin Dist.: Manitoulin Is., South Baymouth, ferry dock, *Ch & R 1271.* **Wisconsin.** Douglas Co.: margins of kettle hole pond by WI-27, WNW of Barnes, *S 9079.*

A. prenanthoides Torr. & Gray. $2n = 32$. **New York.** Cattaraugus Co.: W of Limestone, *S & R 7575.* **Virginia.** Nelson Co.: VA-56 W of Montebello, *S & Ch 5925.*

A. priceae Britt. $2n = 64$. **Tennessee.** Davidson Co.: La Vergne, TN-171 just N of US-41, *S & Ch 9125*; Rutherford Co.: US-70 E of Murfreesboro, 0.4 km W of Baxter Rd., *S & Ch 9126*; near Silver Hill, Al Sup Mill Rd., 0.6 km E of US-231, *S & Ch 9112*; US-231 ca. 5 km S of Vine, *S & Ch 9127.* Wilson Co.: US-231 N of Lebanon, *S & Ch 9128* (white rays), *9130* (blue rays).

Table 1. Continued.

A. puniceus L. $2n = 16$. **Virginia.** Nelson Co.: VA-56 W of Montebello, *S & Ch 5924*.

A. shortii Lindl. $2n = 16$. **Kentucky.** Allen Co.: US-231, just SW of Scottsville, *S & Ch 9106*. $2n = 32$. **Tennessee.** Wilson Co.: SE of Vine, Jennings Pond Rd., 0.5 km E of US-231, *S & Ch 9115*.

A. undulatus L. $2n = 32$. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7661*. **Virginia.** Albemarle Co.: US-29 N of Coveville, *S & Ch 5933*. Northumberland Co.: VA-200 3.6 mi. S of Burgess, *S & Ch 5986*.

Aster other subgenera ($x = 9$)

A. (*Oreastemma*) *alpigenus* (Torr. & Gray) Gray. $2n = 18$. **California.** Siskiyou Co.: Mt. Shasta, meadow by A-10, *8450*. $2n = 36$. Mono Co.: Tioga Pass, 0.25 mi. E of Yosemite National Park, *8688*.

A. (*Eucephalus*) *glaucodes* Torr. & Gray. $2n = 18$. **Utah.** Garfield Co.: UT-12, NE of Tropic, *S & Ch 8902*. San Pete Co.: W of Ephraim, *S & Ch 8890*. Utah Co.: UT-220 13.1 km E of UT-92 E of American Fork, *S & Ch 8880*. Wasatch Co.: UT-220 15 km E of UT-92 E of American Fork, *S & Ch 8879*. **Wyoming.** Albany Co.: US-130 8.5 km W of Centennial, *S & Ch 8862*.

A. (*Doellingeria*) *reticulatus* Pursh. $2n = 9_{II}$. **Florida.** Leon Co.: S of Bloxham, Forest Rd-320 2.2 km W of Forest Rd-344, *S & Ch 9176*; SE of Bloxham, junction of Forest Rds-344 and 304, *S & Ch 9177*. **Georgia.** Colquitt Co.: GA-33 NE of Moultrie, *S & Ch 9171*.

A. (*Eucephalus*) *wasatchensis* (M. E. Jones) Blake. $2n = 18$. **Utah.** Iron Co.: UT-14 26.2 km SE of Cedar City, *S & Ch 8904*.

Aster subg. *Oxytripolium* ($x = 5$)

A. subulatus Michx. var. *ligulatus* Shinners. $2n = 5_{II}$. **Oklahoma.** Atoka Co.: OK-7 just W of Muddy Boggy Creek, W of Farris, *8261*. **Texas.** Stonewall Co.: US-83 N of Aspermont, *8229*.

A. tenuifolius L. var. *tenuifolius*. $2n = 10$. **Maryland.** Queen Annes Co.: US-301 1 km E of drawbridge N of Gasonville, *S & R 7632*.

Benitoa occidentalis (Hall) Keck. $2n = 5_{II}$. **California.** Fresno Co.: CA-198 (NW of MP 9.0) SW of Colwell Rd., *S & Ch 8945*.

Corethrogyne californica DC. var. *obovata* (Benth.) O. Ktze. $2n = 5_{II}$. **California.** Mendocino Co.: CA-1 S of Westport, N of Mackerricher State Park, *8536*.

C. filaginifolia (Hook. & Arn.) Nutt. var. *brevicula* (Greene) Canby. $2n = 5_{II}$. Kern Co.: W of Freeman Junction, CA-178 ca. 17 km W of Onyx, *8650*. $2n = 10$. **California.** Kern Co.: W of Lake Isabella, Kern R. Recreation Area, below main dam, *S & Ch 8951*.

C. filaginifolia (H. & A.) Nutt. var. *peirsonii* Canby. $2n = 5_{II}$. **California.** Kern Co.: S of Tehachapi, Water Canyon Rd., *S & Ch 8958*.

C. filaginifolia (Hook. & Arn.) Nutt. var. *sessilis* (Greene) Canby. $2n = 10$. **California.** San Bernardino Co.: CA-18 2 km E of Santa's Village, *S & Ch 8977*.

C. filaginifolia (H. & A.) Nutt. var. *virgata* (Benth.) Gray. $2n = 5_{II}$. **California.** Monterey Co.: G-18 W of Greenfield, *8608*. San Luis Obispo Co.: Morro Bay, beach dunes N of The Rock, *8618*.

C. leucophylla Jepson. $2n = 5_{II}$. **California.** S of Big Sur, Pfeiffer Beach, *S & Ch 8929*.

Table 1. Continued.

Chrysopsis mariana (L.) Ell. $2n = 4_{II}$. **Florida.** Leon Co.: SW of Bloxham, Forest Rd-320 just E of FL-375, *S & Ch 9175.*

Croptilon divaricatum (Nutt.) Raf. var. *divaricatum.* $2n = 4_{II}$. **North Carolina.** Harnett Co.: NC-27 1.4 km SW of Lillington, *Canne 616.*

Croptilon divaricatum var. *hookerianum* (Torr. & Gray) Shinners. $2n = 12$. **Texas.** Lee Co.: US-77 4.3 mi. N of Giddings (US-290), *S & Bt 3363.*

Eastwoodia elegans Brandegee. $2n = 9_{II}$. **California.** San Joaquin Co.: 17.8 mi. E of Livermore on Co.Rd-J2, *L 3056.*

Ericameria arborescens (Gray) Greene ssp. *arborescens.* $2n = 9_{II}$. **California.** Santa Clara Co.: CA-130 5.1 km E of Mt. Hamilton, *8589.*

E. cuneata (Gray) McClat. $2n = 9_{II}$. **California.** Inyo Co.: W of Lone Pine, Whitney Portal Rd., *8667.* Kern Co.: E of Democrat Springs, between CA-178 and Kern R. 31.2 km SW of CA-155, *S & Ch 8956.* Tuolumne Co.: Pigeon Flat Campground, by Middle Fork of Stanislaus R., E of Dardanelle, *8732.*

E. ericoides (Less.) Jepson. $2n = 9_{II}$. **California.** S of Big Sur, Pfeiffer Beach, *S & Ch 8928.*

E. laricifolia (Gray) Shinners. $2n = 9_{II}$. **New Mexico.** Luna Co.: S of Dening, near entrance to Spring Canyon State Park, *S & Ch 9038.*

E. pinifolia (Gray) Hall. $2n = 18$. **California.** Los Angeles Co.: Claremont, Mt. Baldy Rd. NE of Padua Ave., *S & Ch 8972.*

Erigeron breweri Gray. $2n = 9_{II}$. **California.** Alpine Co.: CA-4 3.5 km E of Lake Alpine, W of Pacific Grade Summit, *8776.*

E. glaucus Ker. $2n = 9_{II}$. **California.** Mendocino Co.: CA-1 S of Rockport, *8532.* Sonoma Co.: CA-1 10.1 km S of county line, Pebble Beach Coastal Access, *8545*; CA-1 6 km N of Bodega Bay, just N of Schoolhouse Beach, *8577.*

E. nematophyllus Rydb. $2n = 9_{II}$. **Wyoming.** Albany Co.: Medicine Bow Nat'l For. 2.5 km by rd. SE of junction of I-80 and Happy Jack Rd., *S 8799.*

E. simplex Greene. $2n = 9_{II}$. **Colorado.** Lake Co.: CO-91 N of Climax below pass, *S 8801.*

E. strigosus Muhl. $2n =$ ca. 9_{II}. **Tennessee.** Morgan Co.: TN-52 ca. 0.5 mi. W of Rugby, *S, Brammall & Hart 3002.*

Euthamia graminifolia (L.) Nutt. $2n = 18$. **New York.** Ulster Co.: NY-52 E of Woodburne, *S, Ch & R 6502.* **Ontario.** Kenora Dist.: junct. Hwy-17 and Mameigwess Rd., *S et al. 6738.* **Vermont.** Addison Co.: VT-125 E of Middlebury, *S 6901.* **Virginia.** Culpepper Co.: VA-3 1.3 mi. NW of Lignum Vitae, *S & Ch 5947.*

E. microcephala Greene. $2n = 18$. **North Carolina.** Wilson Co.: US-117 3.4 mi. N of Wayne Co., S of Wilson, *S & Ch 6012.*

E. occidentalis Nutt. $2n = 9_{II}$. **California.** Mendocino Co.: US-101, Willits, *8554.* San Diego Co.: CA-76 5.7 km NW of CA-79 (Lake Henshaw area), *S & Ch 8988.* $2n = 18$. **California.** Inyo Co.: US-395 N of Lone Pine, S of aqueduct, *8670.* Mono Co.: Topaz, *S & Ch 8907.* San Luis Obispo Co.: Atascadero *8612.* San Mateo Co.: CA-1 7.5 km N of Santa Cruz Co.: 8596. Sierra Co.: CA-49, Fiddler Creek Campground W of Downieville, *8412.* Siskiyou Co.: CA-96 1.6 km W of Horse Creek, *8468.*

Table 1. Continued.

Grindelia inuloides Willd. $2n = 6_{II}$. MEXICO. **Mexico.** Just W of junction of MEX-136 and MEX-85(libre), *L 2396.*

G. oxylepis Greene. $2n = 6_{II}$. MEXICO. **Aguascalientes.** 11.8 mi. W of Ciudad Aguascalientes, *L 2689.* **Jalisco.** MEX-80 9.9 mi. E of Agua el Obispo, *L 2594.*

G. stricta DC. $2n = 12_{II}$. **California.** Mendocino Co.: CA-1 vicinity of Westport Union State Beach, *8534.*

G. subdecurrens DC. $2n = 6_{II}$. MEXICO. **Hidalgo.** Estacion Cazadero, *L 2546.*

Gutierrezia californica (DC.) Torr. & Gray. $2n = 8_{II}$. **California.** Alameda Co.: Corral Hollow Rd. 7.7 mi. W of I-15, *L 2962.* Fresno Co.: CA-198 5.6 mi. SW of CA-33, *L 3055.* Kern Co.: CA-33 9.6 mi. N of CA-46, *L 3033.* San Benito Co.: Clear Creek Rd., 1.8 mi. N of southern end, *L 3036*; 12.6 mi. N of southern end, *L 3037.* Santa Barbara Co.: CA-33 4.1 mi. N of county line, *L 3031.* Stanislaus Co.: Corral Hollow Rd., 3.5 mi. W of I-580, *L 3059.* Yolo/Colusa Cos.: CA-16 0.7 mi. NW of Cache Creek Regional Park (middle site), *L 3043.* $2n = 12_{II}$. **California.** Alameda Co.: East Bay Regional Park, Dunn Trail Loop N of Admin. Bldgs., *L 2959.* Kern Co.: CA-33 2.6 mi. N of Maricopa, *L 3032.* Marin Co.: Angel Island State Park, above Camp Reynolds, *L 3040.* Riverside Co.: CA-74 28.1 mi. E of Kern Camp Summit, *L 3028.* Stanislaus Co.: Arroyo del Seco 6.6 mi. W of Patterson, *L 2961.* Ventura Co.: CA-33 11.4 mi. N of southern boundary of Los Padres Nat'l Forest, *L 3029.*

G. sarothrae (Pursh) Britt. & Rusby. $2n = 4_{II}$. **California.** San Diego Co.: CA-76 0.2 km W of CA-79, *S & Ch 8987.* CA-67 at Posthill Rd. N of Lakeside, *L 3022.* Willows Rd. at I-8, *L 3021.* **Colorado.** Boulder Co.: Boulder, N Gleenwood St. on 30th St., *L s.n.* Moffat Co.: Dinosaur Nat'l Monument, Yampa R. at Deerlodge Campground, *L 2934.* Montrose Co.: Rd-90 (from Naturita to Oak Grove) 2 mi. NE of San Miguel R., *L 2943.* **Idaho.** Bannock Co.: I-15 7 mi. S of Inkom, *L 3049.* **Nevada.** Clark Co.: Christmas Tree Pass Rd. 10.3 mi. E of US-95, *L 3009*; 9.1 mi. E of US-95, *L 3007.* NV-157 2.2 mi. E of US-95, *L 3001.* **Oregon.** Malheur Co.: US-95 22.5 km E of Rome, at Rock Crossing Creek, *L 3051.* US-95 6.5 mi. N of southern end of Succor Creek Recreation Area road, *L 3050.* Morrow Co.: OR-74 2.6 km E of Ione, *L 3054*; 20.1 km S I-84, *L 3055.* **Utah.** Millard Co.: T24S R4 1/2W S9, *L 3047, L 3048.* Uinta Co.: US-40 at mile post 173, *L 2936.* $2n = 8_{II}$. **Arizona.** Maricopa Co.: Vulture Mine Rd. 1.2 mi. S of US-60, *L 2804.* **California.** Riverside Co.: CA-74 21.6 mi. E of Kern Camp Summit, *L 3027.* San Diego Co.: Crestwood Rd. 2.4 mi. S of I-8, *L 3018.* CA-78 6.6 km E of Ramona, *L 3028.* **Oregon.** Gilliam Co.: I-84 11.2 km E of Rufus exit, *L 3052.* $2n = 12_{II}$, 16_{II} (irregular meiosis). **Utah.** Dinosaur Nat'l Monument, Split Mountain Campground, *L 2938.*

G. solbrigii Cabreara. $2n = 20_{II}$. ARGENTINA. **Chubut Prov.**: Pto. Piramides, *H. Cordo s.n.*

G. sphaerocephala Gray. $2n = 4_{II}$. **Texas.** Brewster Co.: Alpine, Sul Ross State University campus, *L 2972.* Hudspeth Co.: US-62 W of Salt Flat, just E of FR-1437, *8159.* $2n = 4_{II} + 0 - 1_{supernumerary}$. **Texas.** Pecos Co.: US-67 2 mi. SW of I-10, *L 2969.*

Table 1. Continued.

Gymnosperma glutinosum (Spreng.) Less. $2n = 8_{II}$. **Texas.** Brewster: 19 mi. N of Alpine, *L 2971*. Jeff Davis Co.: TX-17 13 mi N of Fort Davis, *L 2974*.

Haplopappus gracilis (Nutt.) Nutt. $2n = 2_{II}$. **Arizona.** Cochise Co.: Portal Rd. W of Portal, 1 km W of Research Station of the Amer. Museum Natural Hist., *7993*. **New Mexico.** Luna Co.: S of Denning, near entrance to Spring Canyon State Park, *S & Ch 9037*.

H. havardii Waterfall. $2n = 4_{II}$. **Texas.** Hudspeth Co.: US-62 W of Salt Flat, just E of FR-1437, *8156*.

H. spinulosus (Pursh) DC. $2n = 4_{II}$. **Texas.** Culberson Co.: TX-54 12 km N of Van Horn, *8188*.

H. spinulosus ssp. *australis* (Greene) Hall. $2n = 4_{II}$. **Texas.** Hartley Co.: US-87 8 mi. SE of Dalhart, *S & Shea 1458*.

H. spinulosus ssp. *spinulosus*. $2n = 4_{II}$. **North Dakota.** Sargent Co.: ND-11 1.2 km E of Genesco, *S & Brammall 2686*. **Saskatchewan.** Trans Canada Hwy-1, just E of Balgonie, *S & Shea 1919*; Moose Jaw, 1 mi. W of SASK-2, *S & Shea 1932*; 2 mi. W of Waldeck, *S & Shea 1939*.

H. squarrosus Hook. & Arn. $2n = 5_{II}$. **California.** Monterey Co.: S of Big Sur, Pfeiffer Beach, *S & Ch 8930*.

H. squarrosus Hook. & Arn. ssp. *squarrosus*. $2n = 5_{II}$. **California.** San Luis Obispo Co.: CA-41 just E of Morro Bay, *8616*.

H. squarrosus Hook. & Arn. ssp. *grindelioides* (DC.) Keck. $2n = 5_{II}$. **California.** Santa Barbara Co.: bluffs along US-101 between Gaviota and Refugio State Beach, *8625*. Ventura Co.: CA-150 W of Ojai, *8627*.

Heterotheca grandiflora Nutt. $2n = 9_{II}$. **California.** Tulare Co.: W of Three Rivers, *S et al. 5643*.

H. jonesii (Blake) Welsh & Atwood. $2n = 9_{II}$. **Utah.** Kane Co.: UT-90 ca. 15 mi. W of Mt. Carmel Jct., *S 8829*.

H. rutteri (Rothr. in Gray) Shinners. $2n = 18$. **Arizona.** Santa Cruz Co.: SW of Sonoita, AZ-82 5 km SW of AZ-83, *S & Ch 9030*.

H. zionensis Semple. $2n = 9_{II}$. **Utah.** Kane Co.: UT-9 1 km E of Zion Nat'l Park, *7877*.

Isocoma veneta (H.B.K.) Greene. $2n = 6_{II}$. **California.** San Luis Obispo Co.: CA-41 just E of Morro Bay, *8617*. Santa Barbara Co.: bluff along US-101 between Gaviota and Refugio State Beach, *8626*.

Lessingia nemaclada Greene. $2n = 5_{II}$. **California.** Kern Co.: CA-155 13.9 km E of Glenville, *S & Ch 8948*. Siskiyou Co.: CA-3 SE of Etna, *8497*; CA-96 1.6 km W of Horse Creek, *8467*.

Machaeranthera canescens (Pursh) Gray. $2n = 8$. **Oregon.** Deschutes Co.: US-20 3.6 mi. NW of Sisters, *S & Shea 1984*.

M. grindelioides (Nutt.) Shinners. $2n = 8_{II}$. **Utah.** Garfield Co.: UT-12 S of Boulder, *S 8824*.

Macronema greenei (Gray) Greene. $2n = 9_{II}$. **California.** Glenn Co.: For. Hwy-7 near Mendocino Pass, Plaskett Meadows Recreation Area, *8556*.

M. suffruticosa Nutt. $2n = 9_{II}$. **Nevada.** Washoe Co.: NV-431 at Ophir Creek Trailhead, *8366*.

Table 1. Continued.

Pyrrocoma racemosa (Nutt.) T. & G. var. *sessiliflora* (Greene) Mayes. $2n = 6_{II}$. **California.** Inyo Co.: US-395 just S of L.A. Aqueduct, N of Lone Pine, *8669.*

Solidago altissima L. var. *altissima.* $2n = 27_{II}$. **Illinois.** Bureau Co.: W of Princeton, I-80 9.0 km E of IL-88, *7689.*

S. caesia × *rugosa.* $2n = 18$. **Maryland.** Washington Co.: US-40 N of Greenbrier State Park, *S & R 7657.*

S. californica Nutt. $2n = 18$. **California.** Kern Co.: CA-178 between Onyx and Weldon, *8651.* Riverside Co.: CA-243, Fuller Creek, Lake Fulmore Recreation Area, *S & Ch 8980.* Siskiyou Co.: SE of Etna, CA-3 at rd. to Gazelle, *8498.* CA-96 11 km E of town of Klamath River, *8465.* Sonoma Co.: CA-1 between Valley Ford and Bodega Bay, *8578.* Tuolumne Co.: CA-108 E of Dardanelle (3.7 km E of Kennedy Meadow Rd.), *8730.*

S. canadensis L. $2n = 18$. **California.** Alpine Co. CA-4 E of Pacific Grade Summit E of Bear Valley, *8786.* Butte Co.: between Inship and Butte Meadows at For. Rd. 150b, *8430*; SW of Butte Meadow along Butte Creek, *8431*; Jonesville, *8432.* Calaveras Co.: Poison Spring, W of Bear Valley, *8782.* Mendocino Co.: CA-1 1 km N of Pt. Arena, *8543*; CA-1 4.5 km S of city limit of Pt. Arena, *8550.* Mono Co.: CA-108 0.5 km W of Marine Corps Mountain Warfare Training Center, *8725.* Plumas Co.: Little Grassy Lake Rd. between La Porte and Quincy, *8416.* San Mateo Co.: CA-1 ca. 1 km S of Pescadero State Beach, *8591.* Siskiyou Co.: Etna Summit, SW of Etna on For. Hwy.-93, *8494*; Mt. Shasta City, East Lake St., *8460.* Tulare Co.: T-41 5.0 km W of Sherman Pass Summit E of Johnsondale, *8660.* **Oregon.** Douglas Co.: OR-230 9.7 mi. N of OR-62, *S & Bt 7151B.* $2n = 18_{II}$. **California.** Mendocino Co.: CA-1 10 km N of Cleome, N of MacKerricher State Park, *8537.* $2n = 36$. **California.** Mono Co.: CA-89 4.5 km N of Nevada Co. line, *8403.* **Montana.** Broadwater Co.: US-287 21 mi. E of Townsend, *S & Bt 7007.* $2n = 54$. **Utah.** Juab Co.: Mt. Nebo Scenic Rd., Ponderosa Campground, *S & Ch 8889.*

S. canadensis L. var. *canadensis.* $2n = 18$. **Illinois.** Fulton Co.: US-136 W of Illinois R., *S & Bt 7379.*

S. confinis Gray. $2n = 9_{II}$. **California.** Ventura Co.: Fillmore, Squaw Flat Rd. at N end of A St., *S & Ch 8970.* $2n = 18$. **California.** Riverside Co.: Lake Hemet region, CA-74 6.5 km S of CA-243, *S & Ch 8984.*

S. flexicaulis L. $2n = 36$. **Minnesota.** Mille Lacs Co.: N of Milaca, rest area on US-169, *S 9063.* **Wisconsin.** St. Croix Co.: E of Clifton Spring Golf Course, near Dept. Recreation Boat Access, *S et al. 8856.* Sheboygan Co.: Kettle Moraine State Forest, S of Greenbush Picnic Area, *S 9090.*

S. gigantea Ait. $2n = 18$. **Tennessee.** Marshall Co.: Henry Horton State Park, Wilhoile Mill Hiking Trail, *S & Ch 9118.*

S. glutinosa Nutt. ssp. *glutinosa* var. *glutinosa.* $2n = 18$. **Alaska.** Alaska Hwy (MP1368), NW of Tok, 12 km NW of Dot Lake, just past Berry Bridge, *CC2456.* **Yukon Territory.** Klondike Loop, 12 km S of Pelly Crossing near the 2nd lake, *CC2665.*

S. juncea Ait. $2n = 18$. **Pennsylvania.** Centre Co.: PA-144 2 km S of Potters Mill, *S & R 7604.*

S. lepida DC. $2n = 18$. **California.** Eldorado Co.: CA-89 6 mi. W of Woodford, *S & Ch 8910.* Sierra Co.: CA-49 W of Yuba Pass, *8406.*

Table 1. Continued.

S. aff. *lepida* DC. $2n = 36$. **British Columbia.** Hwy-24 50 km E of Lone Butte, *CC-BC1.*

S. missouriensis Nutt. $2n = 18$. **Wyoming.** Albany Co.: US-130 8.5 km W of Centennial, *S & Ch 8861.*

S. multiradiata Ait. $2n = 18$. **California.** Mono Co.: Lake Mary Rd. ca. 3 km E of Horseshoe L., W of Mammoth Lakes, *8678*; Tioga Pass, just E of Yosemite Park, *8693.* **Utah.** Garfield Co.: ca. 0.5 km W of Hell's Backbone Bridge, N of Escalante, *S & Ch 8901.* San Pete Co.: For. Rd. along crest of Wasatch Plateau, S of For. Rd. to US-89 (E of Manti), *S & Ch 8893.* $2n = 36$. **Alaska.** Steese Hwy, 2 km NE of Captain Creek, 8 km NE of Aurora Borealis Research Station, *CC2396.* **British Columbia.** Haines Hwy 1 km N of Stanley Creek, Chilkat Pass, *CC2524.* **Northwest Territories.** Happy Valley Campground, *CC2634.*

S. nana Gray. $2n = 18$. **Utah.** Dagget Co.: US-191 18.2 km S of Dutch John, *S & Ch 8872.*

S. parryi (Gray) Greene. $2n = 18$. **Wyoming.** Albany Co.: US-130, Snowy Mt. Range, Libby Flats, *S & Ch 8866.*

S. rigida L. ssp. *humilis* (Porter) Heard & Semple. $2n = 9_{II}$. **Wisconsin.** Adams Co.: WI-82, E of Co.Rd-B, *S et al. 8843.* $2n = 18$. **Wisconsin.** Jackson Co.: US-10 8.5 mi. E of Osseo, *S & Ch 5070.*

S. rigida L. ssp. *rigida.* $2n = 18_{II}$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8849.* $2n = 36$. **Wisconsin.** Winnebago Co.: junction of US-41 and WI-110, N of Oshkosh, *S 9088.*

S. rugosa Mill. $2n = 18$. **Illinois.** Jo Daviess Co.: Tapley Woods Forest Res., US-20, *S 9051.* **Maryland.** Cecil Co.: US-1 NE of Rising Sun, *S & R 7617.* **Ontario.** Halton Reg. Mun.: 2.3 km E of Campbellville, *Ch 2233.* Wellington Co.: Belwood Conservation Area, *Ch 2004.* Wentworth Reg. Mun.: Valens Swamp, *Ch 2235.* **Wisconsin.** Crawford Co.: US-61 SE of Soldiers Grove, *S 9052.* $2n = 36$. **Delaware.** New Castle Co.: S of Yorklin, DL-82 ca. 4 km W of DL-52, *S & R 7621.* **Pennsylvania.** Centre Co.: PA-144 W of Pleasant Gap, Nittany Mts., *S & R 7603.*

S. sparsiflora Gray. $2n = 9_{II}$. **Texas.** Culberson Co.: Guadalupe Mt., The Bowl, 7700′, *8182.* $2n = 18$. **Utah.** Utah Co.: American Fork Creek Canyon, 5 km E of UT-92, *S & Ch 8882.* $2n = 36$. **Utah.** Summit Co.: UT-150 12.7 km SE of Kamas, *S & Ch 8886.* Wasatch Co.: UT-220 (MP 22) W of Wasatch Mt. Park, W of Midway, *S & Ch 8876.*

S. spathulata DC. $2n = 9_{II}$. **California.** Mendocino Co.: CA-1 just N of rd. to Pt. Arena Lighthouse, *8542.* $2n = 18$. **California.** Mendocino Co.: CA-1, N of Anchor Bay, ca. 11 km N of Sonoma Co. line, *8548.*

S. speciosa Nutt. $2n = 18$. **Tennessee.** Marshall Co.: between Chapel Hill and Holtland, *S & Ch 9121.*

S. spectabilis (DC. Eaton) Gray. $2n = 18$. **California.** Mono Co.: shore of Mono Lake N of Lee Vining, *8717.*

S. uliginosa Nutt. $2n = 18$. **Wisconsin.** Bayfield Co.: WI-27 21.3 km S of Douglas Co.Rd-A (Barnes), *S 9083.* Douglas Co.: bog along US-2 E of Maple, *S 9072.*

S. ulmifolia L. $2n = 18$. **Illinois.** Adams Co.: Bluff Hall, rd. to church off IL-57,

Table 1. Continued.

S & Bt 7366. **Tennessee.** Marshall Co.: Henry Horton State Park, Wilhoite Mill Hiking Trail, *S & Ch 9119.*

S. wrightii Gray. $2n = 18$. **Arizona.** Yavapai, US-89 NE of Wilhoit, *S & Ch 8997.*

Stephanodoria tomentella (Robinson) Greene. $2n = 6_{II}$. MEXICO. **San Luis Potosi.** Las Tablas, *L 2920*; 0.4 mi. N of Las Tablas, *L 2535*; 0.7 mi. N of Las Tablas, *L 2913*; 300 yd W of Las Tablas, *L 2544.*

Virgulaster ascendens (Lindl.) Semple. $2n = 26$. **California.** Inyo Co.: vicinity of Glacier Lodge, *8673.* $2n =$ ca. 26_{II}. **Utah.** Kane Co.: US-89alt. south edge of Kanab, *7882.*

Virgulus × *amethystinus* (Nutt.) Reveal & Keener. $2n = 10$. **Minnesota.** Pope Co.: Starbuck, *S & Ch 5095.* **Ontario.** North York, *Ch & Cameron 2335.*

V. ericoides (L.) Reveal & Keener. var. *ericoides.* $2n = 10$. **Minneosta.** Crow Wing Co.: MN-371, S of Brainerd, *8794.* Omstead Co.: US-14, SW of Rochester, *S 9053.* **Wisconsin.** Pierce Co.: Co.Rd-F, cliffs W side of Kinnickinnic R., *S et al. 8885.*

V. ericoides var. *pansus* (Blake) Reveal & Keener. $2n = 10$. **New Mexico.** NM-15 39.2 km N of US-180, N of Silver City, *S & Ch 9040.*

V. falcatus (Lindl.) Reveal & Keener. $2n = 10_{II}$. **Colorado.** Lincoln Co.: E of Arriba, I-70 2.6 km E of county line, *7712.*

V. fendleri (Gray) Reveal & Keener. $2n = 10$. **Kansas.** Ford Co.: US-50 0.5 mi. E of county line, *S & Bt 7302.*

V. novae-angliae (L.) Reveal & Keener. $2n = 10$. **Missouri.** Calaway Co.: US-54 1 mi. N of Auxvasse, *S & Ch 5310.*

V. oblongifolius (Nutt.) Reveal & Keener. $2n = 20$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8846.*

V. patens (Ait.) Reveal & Keener var. *phlogifolius* (Muhl.) Reveal & Keener. $2n = 10_{II}$. **Tennessee.** Rutherford Co.: near Silver Hill, Al Sup Mill Rd. 0.6 km E of US-231, *S & Ch 9114.* $2n = 20$. **Kentucky.** Allen Co.: just N of TN border, *S & Ch 9111.*

V. pratensis (Raf.) Reveal & Keener. $2n = 10$. **Florida.** Gadsden Co.: Co.Rd-269 0.5 mi. S of r.r. (River Junction, Chattahoochee), *Godfrey 82636.*

V. sericeus (Vent.) Reveal & Keener. $2n = 10$. **Minnesota.** Hennepin Co.: Eden Prairie, Spring Rd. just W of county airport, *S et al. 8847.* Washington Co.: just N of Stillwater, *S et al. 8858.* **Wisconsin.** Adams Co.: WI-82 1 km E of WI-13, N of Plainville, *S 8842.*

Aster (excluding Virgulaster and Virgulus)

Reports for the genus *Aster* sensu Semple and Brouillet (1980a, 1980b) are listed alphabetically within subgenera. A number of these deserve comment, but most are merely confirmations of previous reports. All reports in Table 1 and previously published reports for *Aster laevis* are $2n = 48$ regardless of variety. The first reports for *A. reticulatus* are in line with all previous reports for members of subg. *Doellingeria* sect. *Triplopappus*.

Numerous chromosome number counts have been reported for members of *Aster* (subg. *Aster* sect. *Dumosi*) subsect. *Porteriani* and were discussed by Semple and Chmielewski (1985). Only the data on *A. priceae* ($2n = 64$, Table 1) represent significant new information; this is the first report of the octoploid level for subsect. *Porteriani* and the species. Semple and Chmielewski (1985) reported a count of $2n = 32$ under the name *A. pilosus* var. *priceae* determined from a plant collected in northeastern Alabama (*S & Ch 6305*). The voucher for the report was re-examined and compared with very typical collections of *A. priceae* from Tennessee as well as the type of the taxon; *6305* is now assigned to *A. pilosus* var. *pilosus*. Thus, we reject our earlier tetraploid report for *A. priceae* and acknowledge that unfamiliarity with the taxon at the time resulted in the misidentification of a rather glabrate, bluish-rayed individual of var. *pilosus*. The tetraploid plant collected in 1981 did not have the decumbent to ascending growth form nor the distinctive bluish-green leaf color typical of the many plants of *A. priceae* we observed in the field at a number of sites in the fall of 1987. The generally larger size of the floral parts of *A. priceae* compared to other species of the subsection can be attributed in part, if not fully, to the higher ploidy level. Ploidy level alone is not likely to be the cause of the other distinctive features of the species. A multivariate morphometric analysis of all taxa in subsect. *Porteriani* is being prepared for submission by J.C.S. and J.G.C. and will more fully explain our decision to accept species status for the octoploid members of the complex.

The count of $3x = 2n = 27$ for *Aster radulinus* from San Mateo Co., California is noteworthy for two reasons. First, reports of triploids in the genus are extremely rare. Second, this is the second report of a triploid in the species; the first triploid was a plant collected in Mendocino Co., California (Semple et al., 1983). Diploids have been reported from two locations in southern Oregon and two locations in southern Washington (Semple, 1985). A pattern is suggested, but the number of reports is still very low. We provisionally suggest that a triploid, apomictic race of the species exists in the Coastal Ranges of California, in the hope of stimulating assistance with additional research on the species.

The $x = 5$ counts for members of *Aster* subg. *Oxytripolium* are in agreement with all previous reports for *A. subulatus* and *A.*

tenuifolius. Semple and Brouillet (1980a) did not exclude the subgenus from *Aster* for nomenclatural reasons, and we have adopted the same policy here. Reasons for excluding the group from *Aster* are discussed below.

Gutierrezia

Counts for the taxa of *Gutierrezia* ($x = 4$) are in keeping with the well documented occurrence of polyploidy in the genus (*see* Lane, 1985). All the South American species are high polyploids, and *G. solbrigii* (a decaploid, reported here for the first time) is no exception. The populations of *G. sarothrae* at Dinosaur National Monument on the Colorado-Utah border included diploid, hexaploid, or octoploid individuals. Meiotic behavior was irregular, indicating that either the polyploids and diploids may not be completely isolated or that the polyploids are unstable. Although the polyploids have been recognized taxonomically (Welsh, 1981), it was deemed wisest to treat the polyploids as *G. sarothrae* (Lane, 1985), until the breeding relationships are understood. A very intensive study of the populations is warranted.

Solidago

Only a few counts for *Solidago* warrant comment. The three tetraploid reports for *S. flexicaulis* listed in Table 1 are from Minnesota and Wisconsin. Semple et al. (1984) and Chmielewski and Semple (1985) noted that on the basis of a limited sample, only tetraploids occurred in the western and southern portion of the range; this finding remains true. For *S. rugosa,* the cytogeographic pattern is altered from that discussed by Semple et al. (1984); the occurrence of diploids in Illinois and Wisconsin (Table 1) indicates that no simple east-west cytotype pattern exists in *S. rugosa*. In the *S. canadensis* complex, diploid and tetraploid counts for populations in California are reported. In most cases these plants are readily assignable to *S. canadensis* ssp. *elongata* (Nutt.) Keck, but the counts are only reported to species in Table 1 due to the uncertain status of infraspecific taxa in the species.

Comments on $x = 6$ Genera and Haplopappus sensu lato

In the first two papers in this series (Semple, 1985; Semple and Chmielewski, 1987) the $x = 6$ taxa included in *Haplopappus* by

Hall (1928) were reported under that generic name in sections *Isocoma, Prionopsis* and *Pyrrocoma.* In Table 1, reports for these $x = 6$ taxa are listed in the appropriate segregate genera following the ideas of M. Lane on phylogeny (Lane and Hartman, 1984, 1985; Lane et al., 1987) based on data indicating that all $x = 6$ taxa in *Haplopappus sensu lato* as well as *Grindelia, Olivaea,* and *Xanthocephalum sensu* Lane (1983) belong to a monophyletic group that does not include *Haplopappus* (*sensu* Table 1; $x = 5$ and derived lower numbers). That *Stephanodoria* also belongs in this group is confirmed here by the counts of $2n = 6_{II}$. Lane and Hartman (1984, 1985) hypothesized that the base number of the genus would be $x = 6$. We do not consider it acceptable to lump all of the taxa in these genera into a single holophyletic genus. Therefore, we have adopted an alternative, which is admittedly a "splitter's" approach to generic limits, at least for the present, pending the results of research now in progress by other laboratories (University of Texas and University of Kansas) on chloroplast DNA restriction fragment polymorphisms.

Reports for $x = 9$ taxa included in *Haplopappus sensu* Hall (1928) are listed in Table 1 under *Ericameria* and *Macronema.* The species in these two genera, and those in *Chrysothamnus,* form a natural alliance that cannot be separated into well-defined groups worthy of generic recognition, unless arbitrary character limits are adopted. We think that all taxa probably should be included under a single generic name, *Chrysothamnus,* once nomenclatural priorities have been sorted out fully in studies in progress. Since the appropriate combinations are not yet available, the chromosome number reports are given under the segregate generic names.

Generic Limits and the Ancestral Base Number of the Astereae

Our acceptance of a number of segregate genera is based on opinions favoring an $x = 5$ ancestral chromosomal base number for the entire tribe Astereae. Recognition of *Virgulus* (ancestrally $x = 5$) separate from *Aster* (ancestrally $x = 9$) continues in this paper. This separation raises the philosophical problem of how to deal nomenclaturally with the species first described as *Aster ascendens* Lindl. ($x = 13$; $n = 13, 26$), which Allen (1985) demonstrated to be of allopolyploid origin. The putative parents were *A. occidentalis* Nutt. ($x = n = 8$) and *V. falcatus* (Lindl.) Reveal

& Keener ($x = n = 5$; treated as *A. falcatus* by Allen). The $x = 13$ base number is unique in the tribe, and for this reason its origin is a special phenomenon that ought not to be dismissed casually on the grounds that asters are notorious for hybridizing. Admittedly, *Virgulaster ascendens* (Lindl.) Semple, the name under which counts for the species are reported in Table 1, is very similar morphologically to its putative $x = 8$ parent. However, the species includes the $x = 5$ as well as the $x = 8$ genome and both are reflected in its morphology, which is to be expected in an allopolyploid. If *Virgulus* is viewed as a concept that has irretrievably floundered "on the rocks of allopolyploidy" (Cronquist, 1985), then *Virgulaster* must be submerged as well. If this case of allopolyploidy is recognized for its special nature, a high peak in cytological evolution within the tribal landscape, then its existence does not mean that *Virgulus* must be abandoned. Cytological data can be seminal in understanding phylogenetic relationships in the Astereae that subsequently have been supported by previously overlooked morphological data; for example, separation of *Heterotheca* sect. *Phyllotheca* form *Chrysopsis* (*sensu* Semple et al., 1980) and the recognition of the virguloid asters (regardless of rank) as a distinct phylad of asters (Jones, 1980a, 1980b; Semple and Brouillet, 1980a, 1980b). Nomenclature must reflect phylogeny, if it is to be useful in predicting degrees of similarity in unexplored data bases. *Virgulus* may not be convenient as a generic concept, but it does provide a label for a monophyletic assemblage whose phylogenetic relationships to other taxa, including other asters, are not really understood. There are no data that conclusively show that *Virgulus* is derived from *Aster* via dysploidy (the latter being paraphyletic), or that *Aster* is derived in part or fully from *Virgulus* via allopolyploidy, or that either is ancestral to the other (the least likely option on the basis of morphology). Also, it is not clear how the oxytripolioid asters fit into the phylogeny. Pragmatically, use of the name *Virgulus* ensures that an $x = 5$ species in the genus is not included in studies as representative of the ancestrally $x = 9$ *Aster* (*sensu* Semple and Brouillet, 1980a, 1980b). For the same reason, *A.* subg. *Oxytripolium* (ancestrally $x = 5$; discussed below) also should be treated as a separate genus, but it is not for nomenclatural reasons.

Choice of $x = 9$ taxa to be included in studies on the ancestral chromosomal base number of the tribe is important. The phylogenetic position of *Aster pauciflorus* Nutt. (synonym: *A. hydrophilus* Greene) is critical in the interpretation of the results of some studies concerned with the base number question (Stucky and Jackson, 1975; Stucky, 1978; Gottlieb, 1981). The assumption has been made that *A. pauciflorus* is representative of the $x = 9$ species of *Aster,* at least in terms of genomic evolution, and that it is not a recently derived allopolyploid. If the species falls in the latter category, it is a most inappropriate organism for testing hypotheses on the numbers of gene loci to be expected in the higher base number taxa of the tribe (Gottlieb, 1981). Phyllary shape and margin features, rhizome features and the preference for brackish wetland habitats suggest a relationship between *A. pauciflorus* and the $x = 5$ members of *Aster* subg. *Oxytripolium* (*A. subulatus* and *A. tenuifolius,* Table 1). Jones (1980a, 1980b) treated *A. pauciflorus* as a member of the subgenus on the basis of unspecified morphological similarities. If *A. pauciflorus* is closely related to the oxytripolioid asters, then it is an allopolyploid with the $x = 4$ portion of the genome possibly coming from *Machaeranthera* sect. *Psilactis.* The chromosome pairing reported by Stucky and Jackson (1975) may reflect such an origin in the same manner that chromosome pairing between $x = 5$ and $x = 9$ taxa in *Chrysopsis* demonstrated the allopolyploid nature of the higher base number species (Semple and Chinnappa, 1980a, 1980b). One difference in the two cases involves the size of the derived genome which was greatly reduced in the case of *Aster pauciflorus,* but not in *Chrysopsis gossypina* (Michx.) Ell. Relevant are the unpublished data of a preliminary examination of gene loci number in *Chrysopsis.* Gottlieb (pers. comm. to J.C.S.) found no evidence to support the polyploid status of *C. gossypina,* but the results were "consistent with the hypothesis that the different chromosome numbers reflect aneuploid changes." However, cytological studies (Semple and Chinnappa, 1980b) clearly demonstrated that the $x = 9$ base number was of alloploid origin. Thus, the electrophoretic data turned out to be unrevealing in the case of *Chrysopsis.* In the case of *A. pauciflorus,* we believe similar results have been cited as evidence supporting an $x = 9$ ancestral base number for the tribe. Until a study is done involving other $x = 9$ species of *Aster* which are not putative recently-derived allopolyploids, it seems most reasonable to accept that the ancestral base number question, $x = 5$ versus $x = 9$, has not been resolved satisfactorily by electrophoretic or chromosome pairing data published to date. Minimally, the uncertain phylogenetic position of *A. pauciflorus* disqualifies it as the species on which to rest conclusions about the ancestral base number of the Astereae. Whether $x = 5$ or $x = 9$ is ancestral in the Astereae is very important in setting generic limits and constructing phylogenies. If $x = 9$ is ancestral as suggested by Raven et al. (1960), then all lower base number taxa must be derived a number of times from higher base number taxa. If $x = 5$ is ancestral as suggested by Turner et al. (1961), then the several $x = 9$ phylads must be polyploid, including *Aster sensu* Semple and Brouillet (1980a). At present, the more frequently used nomenclatural schemes recognize a few large genera, such as *Haplopappus* (*sensu* Hall, 1928). These nomenclatural systems were proposed before cytological data were available, and thus they do not reflect the implications of such data. Nomenclature should reflect all information available, for this reason we have adopted unconventional, narrow generic limits in this paper.

We conclude with a cautionary note about resolving phylogenetic and nomenclatural problems in the Astereae via restriction enzyme fragment polymorphism data. Any data base that only can reveal the maternal line in a phylad cannot be relied upon alone to sort out patterns of reticulate evolution, although knowing conclusively the identity of one parent of an allopolyploid phylad will be very informative. Just as electrophoretic data have not been as conclusive as we might wish, so too will DNA studies in some cases provide ambiguous results in the Astereae and elsewhere.

ACKNOWLEDGMENTS

This work was supported in part by Natural Sciences and Engineering Research Council of Canada Operating Grants to J.C.S. and by a National Science Foundation of the United States grant (BSR-8508631) to M.A.L. The following people are thanked for their assistance in the field: Dr. L. Brouillet, David Farris, Stephen Heard, Dr. G. Ringius, and Jeff Semple. Viable achenes sent by Don Baker, Dan Brunton, and Dr. R. Godfrey were much appreciated. The collection of *Gutierrezia solbrigii* from Argentina was provided by Hugo Cordo. Collections from Dinosaur National Monument, Guadalupe Mountain National Park, and Angel Island State Park were taken under permit.

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